



Grassland degradation significantly enhances soil CO₂ emission

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ABSTRACT

Grassland degradation reduces net primary production and, subsequently, soil fertility and soil organic carbon stocks (SOCs); however, little is known about its impact on soil CO₂ emissions, particularly the emissions relative to SOCs and biomass produced. The main objective of this study, performed in KwaZulu-Natal province of South Africa, was to quantify the impact of grass basal cover, as main indicator of grassland degradation, on soil CO₂ emissions. The soil CO₂ emissions were measured from three grass cover levels (non-degraded, with 100% grass cover; moderately degraded: 25 < grass cover < 50%; and highly degraded: 0 < grass cover < 5%) using a LI-COR 6400XT. The measurements were done at three randomly selected positions in each grass cover level, from January 2013 to April 2015. At each position, measurements were done once during winter months and twice during summer months, resulting in a total of 1053 measurements for the entire study period. The measured average gross soil CO₂ emission was significantly higher ($1.78 \pm 0.013 \text{ g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$) in non-degraded than moderately ($1.60 \pm 0.12 \text{ g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$) and highly degraded grasslands ($0.68 \pm 0.10 \text{ g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$). However, when expressed relative to SOCs and aboveground biomass produced, the trends were opposite. Average soil CO₂ emission relative to SOCs was lowest in the non-degraded grassland ($0.034 \pm 0.01 \text{ g CO}_2\text{-C g}^{-1} \text{ C day}^{-1}$) and highest in the moderately degraded grassland ($0.058 \pm 0.02 \text{ g CO}_2\text{-C g}^{-1} \text{ C day}^{-1}$) with the highly degraded grassland being intermediate ($0.04 \pm 0.00 \text{ g CO}_2\text{-C g}^{-1} \text{ C day}^{-1}$). Similarly, soil CO₂ emission relative to aboveground biomass produced was lowest in the non-degraded grassland at $0.15 \pm 0.02 \text{ kg CO}_2\text{-C kg}^{-1} \text{ biomass year}^{-1}$, which was almost 5 fold lower than $0.73 \pm 0.01 \text{ kg CO}_2\text{-C kg}^{-1} \text{ biomass year}^{-1}$ in the highly degraded grassland. Gross soil CO₂ emission correlated significantly and positively with SOC ($r = 0.83$ and 0.82 for SOC content and stocks, respectively), SON (0.67 and 0.53 for content and stocks, respectively), C:N ratio (0.62), and soil water content (0.75) but negatively with clay content (-0.89). Soil CO₂ emission relative to SOCs correlated significantly and negatively with both SOC (-0.50 and -0.51 for content and stocks, respectively) and SON (-0.45 and -0.42 for content and stocks, respectively). While gross CO₂ emissions decreased with grassland degradation, CO₂ emission relative to both SOCs and aboveground biomass increased with grassland degradation. These results point to direct links between grassland degradation and global warming because CO₂ is one of the key greenhouse gases. Therefore, strategies for rehabilitating degraded grasslands need to aim at reducing soil CO₂ emission in order to mitigate climate change.

1. Introduction

The increasing atmospheric greenhouse gas concentration, due to anthropogenic disturbances, is a matter of great concern. Grasslands play a crucial role in the global carbon (C) cycle as they cover 40% of the world surface area and store about 10% of the soil C stock of 2400 Pg (1 Pg = 10^{15} g = 1 billion tons) (Suttie et al., 2005). Land degradation, defined as a process which lowers the capability of soils to

produce food and fodder (FAO, 1979), is generally attributed to human activities, especially changes in land use and/or land mismanagement (Shang and Long, 2007; Gang et al., 2014; Fassnacht et al., 2015). Approximately 50% of global grasslands are reportedly already degraded (Gang et al., 2014). Grassland degradation, generally regarded a reduction in soil basal cover, has well-known negative consequences on grass production and biodiversity (UNEP, 2007; Dong et al., 2012). The reduction in soil basal cover results in significantly lower soil

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infiltration by water. Reduced infiltration, in turn, induces soil C erosion (Mchunu and Chaplot, 2012), which reduces soil organic carbon stocks (SOCs) (Dlamini et al., 2014), water content (Yi et al., 2012) and soil temperature (Mills and Fey, 2004).

Several studies have extensively investigated the impact of grassland degradation on SOC stocks (SOCs). For instance, Dlamini et al. (2016) in a meta-analysis of 131 comparative studies worldwide showed that grassland degradation reduces SOCs by an average 9%, with 16 and 8% reductions in dry and wet climates, respectively. Dong et al. (2012) also reported significant decline (33%) of SOC with increasing degradation in the Qinghai-Tibetan Plateau of China. In addition, Dlamini et al. (2014) reported SOCs loss of as much as 89% following degradation of grassland in the sub-tropical climate of South Africa. While these studies and numerous others reported on the impacts of grassland degradation on SOCs, there are very few studies reporting on the consequences on soil CO₂ emissions. For example, Rey et al. (2011) reported 25% higher soil CO₂ emissions from non-degraded than degraded grasslands in Southeastern Spain. Traoré et al. (2015) reported as much as 82% higher soil CO₂ emissions from non-degraded than degraded grasslands in semi-arid West Africa. In contrast, some studies reported more soil CO₂ emissions from degraded than non-degraded grasslands (Cao et al., 2004; Li et al., 2015; Chen et al., 2016). For example, Chen et al. (2016) reported 23.6% more annual CO₂ fluxes from degraded than non-degraded soils. Li et al. (2015) reported similar findings, which they explained to be a result of higher soil temperatures leading to greater C mineralization. The contradicting results on the impact of grassland degradation on soil CO₂ emissions might require further appraisal. Work is also still required to inform on the impacts of grassland degradation on soil CO₂ emission relative to SOCs and biomass production. The CO₂ emission relative to SOCs and biomass produced could serve as indirect means of evaluating SOC stability and the economic use of C by grasslands, respectively, which are further indicators of ecosystem functioning. In addition, knowledge on the factors controlling soil CO₂ emissions following grassland degradation is important during formulation of strategies to minimize soil CO₂ emissions by maximizing soil C protection and/or sequestration, and biomass production. Therefore, the present study performed on a grassland in KwaZulu-Natal, South Africa, aimed to assess soil CO₂ emission as a function of grass basal cover, SOCs, grass production and a series of environmental and soil properties. The study hypothesis was that low basal cover increases soil temperature, which in turn enhances soil C mineralization to yield higher soil CO₂ emission than under non-degraded grasslands.

2. Materials and methods

2.1. Study area

The experiment was conducted at Potshini (29° 21' E, 28° 48' S; altitude range 1080–1455 masl), located 10 km south of Bergville town in KwaZulu-Natal province, South Africa. The area experiences a temperate climate characterised by warm wet summers and cool dry winters. The long-term (30 years) mean annual temperature and precipitation of the study area are 13 °C and 684 mm, respectively (Dlamini et al., 2011). Moist Highveld Sourveld dominated the native vegetation of this area (Camp and Hardy, 1999). The experimental site was located on a hillslope of about 10% slope gradient. The site exhibited a grassland degradation gradient where soil basal cover decreased in an upslope direction. Its soils were classified as *Plinthic Acrisols* (WRB, 2006) derived from sandstones and mudstones. More details about the study site characteristics are in Dlamini et al. (2014), Mchunu and Chaplot (2012) and Podwojewski et al. (2011).

2.2. The experimental design

Dlamini et al. (2011) initiated the experiment, in a rural

community, with the aim of investigating potential techniques for rehabilitating degraded communal grasslands. An area measuring 1500 m² (30 m × 50 m) and showing morphologically, chemically and physically homogeneous soils was demarcated. This area also showed grassland degradation intensities with the downslope position non-degraded (grass aerial cover, of 100%), the mid-slope moderately degraded (25 < grass cover < 50%), while the upslope position was highly degraded (0 < grass cover < 5%) (Mchunu and Chaplot, 2012; Dlamini et al., 2014). The demarcated area was further divided into several upslope-downslope swaths so that each swatch, treated to a specific grassland management technique, covered all three grass cover levels (Dlamini et al., 2011; Mchunu and Chaplot, 2012; Dlamini et al., 2014). The current study measured soil CO₂ emissions from a ring-fenced swath to eliminate any interaction with livestock, fires or any other significant disturbance. The soil CO₂ measurements were performed at three randomly selected positions per grass cover level. A plastic (PVC) collar (diameter = 10 cm, height = 4 cm) was set up at each position. The PVC collars were inserted 2 cm into the soil between grass tufts, two weeks before the first CO₂ emission measurements of to avoid errors associated with soil disturbance (Hui-Mei et al., 2005; Heinemeyer et al., 2011).

2.3. Soil CO₂ emission measurements

The soil CO₂ emission measurements were performed using a LI-COR 6400XT gas analyzer (LI-COR, Lincoln, NE, USA) fitted with a LI-COR 6400-09 soil respiration chamber. The closed chamber system had an internal volume of 991 cm³ and a surface area of 71.6 cm² (Healy et al., 1996). Immediately before CO₂ measurement, the chamber was positioned on the PVC collar. The measurements were performed once a month during dry winters and twice a month in wet summers, from January 2013 to April 2015. Three readings were recorded per measuring position during each measurement session. Thus, 1053 soil CO₂ emission records were generated in 39 days that the experimental site was visited for the purpose of measuring soil CO₂ emissions. On each day, CO₂ measurements were performed between 10.00 and 13.00 h to avoid strong influences of diurnal variations. The CO₂ fluxes, measured by the LI-COR, were converted to CO₂-C based on atomic weights of C and oxygen. The fluxes were subsequently expressed in (i) gross soil CO₂ emission: g CO₂ per unit of surface area (g CO₂-C m⁻² day⁻¹); (ii) soil CO₂ emission relative to SOCs: g CO₂ per gram of soil C (g CO₂-C g⁻¹ C day⁻¹); and (iii) soil CO₂ emission relative to amount of aboveground biomass produced: g CO₂ per kg of aboveground biomass (g CO₂-C kg⁻¹ produced biomass year⁻¹).

2.4. Soil temperature and soil water content

Topsoil (0–0.05 m) temperature and water content were measured in conjunction with soil CO₂ emissions. Temperature was measured using a thermocouple connected to the LI-COR chamber. Water content was measured using a Hydrosense soil moisture meter (Campbell Scientific, Inc., USA), which was calibrated at the study site. The soil temperature and water content measurements were performed at randomly selected positions within a 0.2 m radius from each PVC collar.

2.5. Soil sampling and analysis

Topsoil (0–0.05 m) samples were collected for evaluating SOC (SOC_C) and soil organic nitrogen (SON_C) contents. Sampling was performed in June 2014. Three replicate samples were collected from randomly selected positions 0.2–1 m from each PVC collar. The samples were first air-dried for 48 h, before gently grinding and sieving them through a 2 mm sieve. The soil particle size distribution was determined on the sieved samples using the pipette method (Gee and Bauder, 1986). Total C and nitrogen content were measured using LECO CNS-2000 Dumas dry matter combustion analyzer (LECO Corp., St. Joseph,

MI). The total soil C was considered equivalent to SOC_c since no reaction was obtained following addition of HCl. SOC_s and SONs (SON stocks) were calculated using the equation by Batjes (1996):

$$\text{SOC}_s = \text{SOC}_c \times \rho_b \times T \left(1 - \frac{\text{PF}}{100} \right) b$$

where SOC_s is the soil organic carbon stock (kg C m^{-2}); SOC_c is soil organic carbon content in the ≤ 2 mm soil material (g C kg^{-1} soil); ρ_b is the bulk density of the soil (kg m^{-3}); T is the thickness of the soil layer (m); PF is the proportion of fragments of > 2 mm in percent; and b is a constant equal to 0.001.

The soil bulk density was determined from undisturbed soil samples collected by inserting metallic cylinders of 7.5 cm diameter and 5 cm height into the topsoil layers. The undisturbed samples were stored in hermetic plastic cans immediately after collection and later dried in an oven at 105 °C for 24 h. The soil bulk density was determined according to Grossman and Reinsch (2002).

2.6. Aboveground biomass

The aboveground biomass ($\text{kg m}^{-2} \text{ year}^{-1}$) was evaluated in three randomly placed metallic quadrats ($0.5 \text{ m} \times 0.5 \text{ m}$) in each grass cover

level within a distance of 0.2 to 1 m radius from the CO_2 emissions measurements collars at peak biomass in June 2013 and 2014. All shoot material from the soil surface to the crown within the quadrats was clipped. The plant samples were oven-dried at 70 °C and then weighed until constant weight.

2.7. Statistical analysis

Overall mean and standard error were calculated for gross soil CO_2 emissions, and soil CO_2 emissions relative to SOC_s and biomass production for the three grass cover levels. Since the soil CO_2 emission measurements were performed at regular time intervals from the same points, the data were statistically analysed using repeated-measures analysis of variance. The average soil CO_2 emissions for the grass cover levels were compared using Tukey's for multiple comparisons, a significant threshold defined as $P < 0.05$, unless otherwise specified. In addition, cumulative soil CO_2 emissions were also analysed using REML repeated measure ANOVA. The final cumulative values were compared using the Tukey test. All analyses were performed using Genstat (version 14, VSN International, UK, 2011). In addition, coefficients of determination (r) and principal component analysis (PCAs) were carried out to evaluate the relationships between the

Table 1

Mean and standard error (SE) for CO_2 emissions from non-degraded (ND), moderately degraded (MD) and highly degraded (HD) grasslands.

	Gross soil CO_2 ($\text{g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$)			Soil CO_2 relative to SOC _s ($\text{g CO}_2\text{-C g}^{-1} \text{C day}^{-1}$)			Soil CO_2 relative to biomass ($\text{g CO}_2\text{-C kg}^{-1} \text{ biomass yr}^{-1}$)		
	ND	MD	HD	ND	MD	HD	ND	MD	HD
Mean	1.78a	1.60b	0.68c	0.034c	0.058a	0.040b	0.15c	0.54b	0.73a
SE	0.13	0.12	0.10	0.00	0.01	0.00	0.05	0.06	0.01

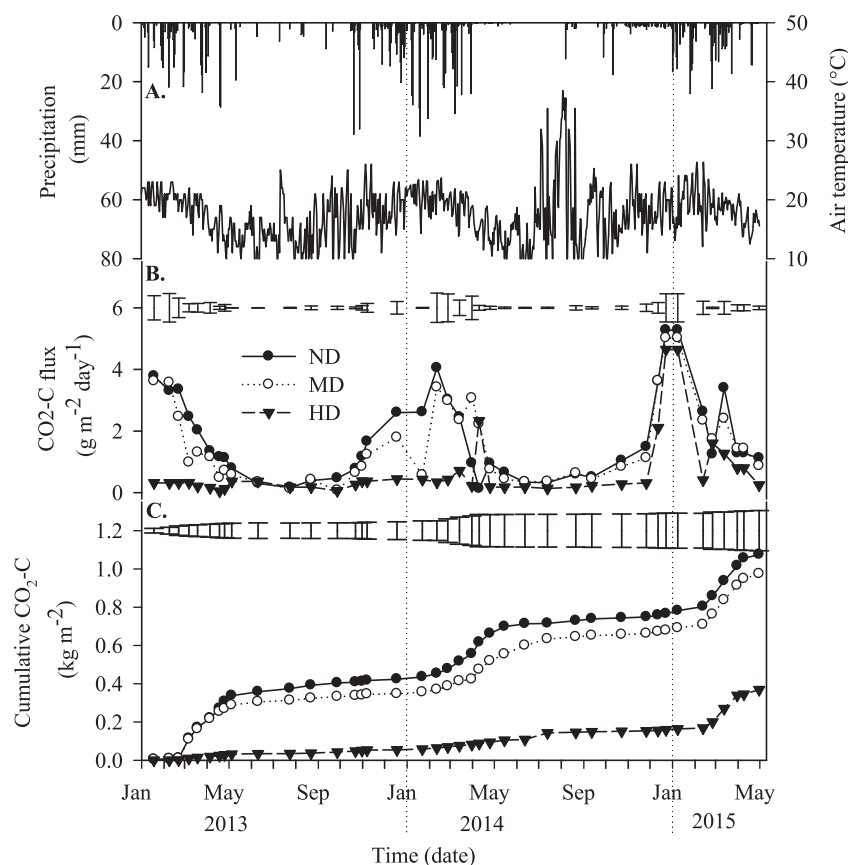


Fig. 1. Rainfall, air temperature, daily fluxes and cumulative gross $\text{CO}_2\text{-C}$ ($\text{g CO}_2\text{-C m}^{-2}$) from soil, over the study period from non degraded (ND), moderately degraded (MD) and highly degraded (HD) grassland. Error bars represent \pm one standard error of the difference. $N = 9$.

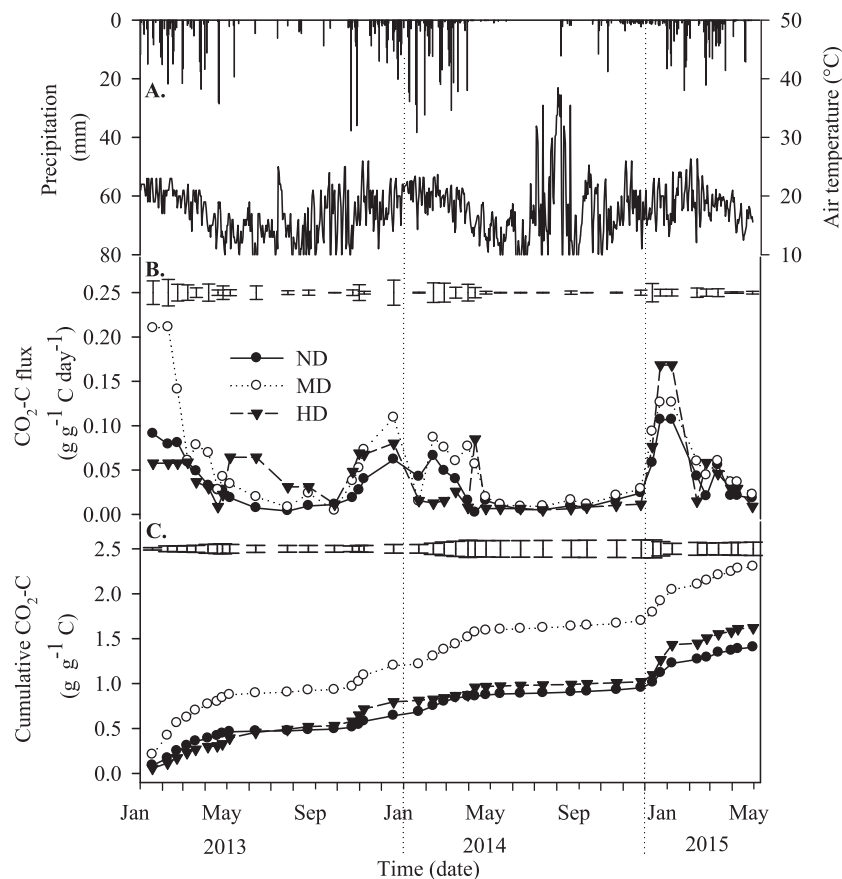


Fig. 2. Rainfall, air temperature, daily fluxes and cumulative of $\text{CO}_2\text{-C}$ from soil relative to soil organic carbon stocks ($\text{g CO}_2\text{-C g}^{-1}\text{C}$) over the study period from non degraded (ND), moderately degraded (MD) and highly degraded (HD) grassland. Error bars represent \pm one standard error of the difference. $N = 9$.

soil CO_2 emissions and selected control factors.

3. Results

3.1. Impact of grassland degradation on soil CO_2 emission

The study period mean daily gross soil CO_2 emissions was 11 and 62% higher in non-degraded ($1.78 \pm 0.13 \text{ g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$) than moderately and highly degraded grassland, respectively (Table 1). Gross soil CO_2 fluxes varied in response to both precipitation and air temperature (Fig. 1A), but were generally higher in non-degraded than moderately and highly degraded grasslands (Fig. 1B). The annual precipitations were 718 and 562 mm in 2013 and 2014, respectively, with about 90% of the precipitation occurring in summer (November to April). The mean annual air temperature was 17°C for both years. Differences in gross soil CO_2 emissions between non-degraded and highly degraded grasslands were only significant during 17 of the 39 sampling events, mostly in summer. The final cumulative soil CO_2 emission was highest under non-degraded grassland ($1.12 \pm 0.02 \text{ kg CO}_2\text{-C m}^{-2}$) (Fig. 1C). However, this was not significantly different from that of moderately degraded grassland ($0.97 \pm 0.13 \text{ kg CO}_2\text{-C m}^{-2}$). Nevertheless, the final non-degraded grassland cumulative gross soil CO_2 emissions was 62% higher than on non-degraded grassland.

In contrast, soil CO_2 emission relative to SOC_s was significantly higher in both moderately ($0.058 \pm 0.005 \text{ g CO}_2\text{-C g}^{-1}\text{C day}^{-1}$) and highly degraded grasslands ($0.040 \pm 0.004 \text{ g CO}_2\text{-C g}^{-1}\text{C day}^{-1}$) than non-degraded grassland ($0.034 \pm 0.002 \text{ g CO}_2\text{-C g}^{-1}\text{C day}^{-1}$) (Table 1). This result indicates that soil CO_2 emission relative to SOC_s increased by 71% from non-degraded to moderately degraded grassland, and by only 18% from non-degraded to highly degraded

grassland. The soil CO_2 emissions relative to SOC_s also varied over time with both precipitation and temperature (Fig. 2A). Moderately degraded grassland had generally higher soil CO_2 fluxes, especially during summer months (October to April); however, soil CO_2 emission differences between grass cover levels were only significant for 5 of the 27 summer sampling events (Fig. 2B). The cumulative soil CO_2 emission relative to SOC_s was highest in moderately degraded grassland ($2.3 \pm 0.12 \text{ g CO}_2\text{-C g}^{-1}\text{C}$), followed by highly degraded ($1.6 \pm 0.18 \text{ g CO}_2\text{-C g}^{-1}\text{C}$) and least in the non-degraded grasslands ($1.4 \pm 0.09 \text{ g CO}_2\text{-C g}^{-1}\text{C}$) (Fig. 2C). However, there was no significant difference between highly degraded and non-degraded grassland.

Overall, average soil CO_2 emission relative to aboveground biomass was lowest in the non-degraded grassland at $0.15 \pm 0.05 \text{ kg CO}_2\text{-C kg}^{-1} \text{ biomass year}^{-1}$ (Table 1). This was almost 3.5 and 5 fold lower than in moderately and highly degraded grasslands, respectively. The cumulative soil CO_2 emission relative to yearly produced biomass was also significantly higher under highly degraded than non-degraded grassland, at about 613% by end of the second year of the survey (2014–2015). While, there was no significant soil CO_2 emission relative to biomass difference between moderately degraded and highly degraded grasslands in the first production cycle, the two differed by 47% in the second production cycle with the highly degraded grassland having higher emission.

3.2. The impact of grassland degradation on soil properties and biomass production

3.2.1. Soil organic carbon and nitrogen

Mean soil organic C stocks (SOC_s) and content (SOC_c) were

Table 2

Coefficients of determination (r) between gross soil CO_2 emission ($\text{g CO}_2\text{-C m}^{-2}$) and soil CO_2 emission relative to soil carbon stocks ($\text{g CO}_2\text{-C g}^{-1}\text{C}$) from soils and multiple factors: soil organic carbon content and stocks (SOCc and SOC_s), soil organic nitrogen content and stocks (SONc and SON_s), carbon: nitrogen ratio (C:N), soil bulk density (ρ_b), clay content, soil water content (SWC), soil temperature (ST) and aboveground biomass (AGB).

	SOCc	SOC _s	SONc	SON _s	C:N	ρ_b	Clay	SWC	ST	AGB
$\text{g CO}_2\text{-C m}^{-2}$	0.83 ^a	0.82 ^a	0.67 ^a	0.53 ^a	0.62 ^a	−0.22	−0.89 ^a	0.75 ^a	−0.12	0.37
$\text{g CO}_2\text{-C g}^{-1}\text{C}$	−0.50 ^a	−0.51 ^a	−0.45 ^a	−0.42 ^a	−0.29	0.02	−0.18	−0.17	0.22	0.00

^a Statistically significant determinants at $P < 0.05$.

highest in non-degraded grassland soils and least in highly degraded grassland soils (Fig. 4A–B). The non-degraded grassland SOC_s were 176% higher than in moderately degraded grassland, and 754% higher than in highly degraded grassland (Fig. 4A). The SOC_c also decreased with increasing grassland degradation, in the following order; non-degraded ($15.72 \pm 0.58 \text{ g kg}^{-1}$) > moderately degraded ($5.69 \pm 0.66 \text{ g kg}^{-1}$) > highly degraded ($1.84 \pm 0.18 \text{ g kg}^{-1}$) (Fig. 4B).

Soil organic nitrogen stocks (SON_s) and content (SON_c) followed a similar behaviour by decreasing from non-degraded to highly degraded grassland (Fig. 4C–D). The non-degraded grassland SON_s were 167% higher than highly degraded grassland (Fig. 4C). The SON_c decreased sharply from non-degraded to moderately degraded grassland before decreasing further in the highly degraded grassland; however, there was no significant difference between moderately and highly degraded grasslands (Fig. 4D).

3.2.2. Soil bulk density and clay content

Soil bulk density tended to increase with grassland degradation, from an average of 1.3 g cm^{-3} in non-degraded grassland to 1.5 g cm^{-3} in highly degraded grassland (Fig. 4E). However, there was no significant difference between moderately and highly degraded grasslands. It was interesting that topsoil (0–0.05 m) clay content increased with grassland degradation (Fig. 4F), meaning that the topsoil clay content increased in an upslope direction. Non-degraded grassland clay content was 36 and 59% lower than moderately and highly degraded grasslands, respectively.

3.2.3. Soil water content and temperature

Overall, average topsoil water content was highest in non-degraded and lowest in highly degraded grassland (Fig. 5A), implying lower water retention with lower vegetation cover. However, there was no significant difference between non-degraded and moderately degraded grasslands. The overall mean topsoil temperature was highest in moderately degraded grassland (25.8°C) and lowest in highly degraded grassland (21.8°C) (Fig. 5B). There was also no significant difference between non-degraded and moderately degraded grasslands. The temporal evolution of soil temperature changed markedly over time (Fig. 6). The lowest temperature amongst the degradations levels was 8°C observed in July of 2013 and 2014, in highly degraded grassland, and the maximum temperature was 45°C observed in February 2015, in moderately degraded grassland.

Table 3

Repeated-measures ANOVA for the effects of grassland degradation, date of CO_2 sampling and their interaction on CO_2 flux.

Source of variation	DF	$\text{g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$		$\text{g CO}_2\text{-C g C}^{-1} \text{ day}^{-1}$	
		MS	P	MS	P
Degradation	2	41.80	< 0.001	0.018	< 0.001
Time	39	11.64	< 0.001	0.010	< 0.001
Degradation * Time	78	01.36	< 0.001	0.002	< 0.001

DF: degree of freedom.

3.2.4. Aboveground biomass production

Average annual aboveground biomass for the different grassland degradation intensities during the study period are shown in Fig. 7. As expected, non-degraded grassland had the highest biomass production of $3.28 \pm 0.42 \text{ kg m}^{-2} \text{ year}^{-1}$, which was 55 and 81% higher than for moderately and highly degraded grassland, respectively. This result was consistent with trend in soil water content (Fig. 5A) and implied greater soil fertility in non-degraded than the moderately and highly degraded grassland sites.

3.3. Controls of soil CO_2 emissions

Gross soil CO_2 emissions increased significantly with SOC content and stocks ($r = 0.83$ and 0.82 , respectively) (Table 2). Soil organic nitrogen ($r = 0.67$ and 0.53 for SON_c and SON_s, respectively) and water content (0.75) showed strongly positive correlations with gross soil CO_2 emission as well. However, gross CO_2 emission decreased significantly with clay content (-0.89). On the other hand, soil CO_2 emission relative to SOC_s decreased with both SOC_c ($r = -0.50$), SOC_s (-0.51), SON_c (-0.45) and SON_s (-0.42). The repeated ANOVA results indicated that grasslands degradation level, date of CO_2 measurement and the interactions between them also had highly significant effects ($P < 0.001$) on the soil CO_2 emissions (Table 3).

Axis 1 and 2 of the first PCA explained 77% of the total variation of the dataset (Fig. 8A). Axis 1, which described 44% of the variance, was positively correlated to SOC_c, SOC_s, SON_c, C:N ratio and SON_s (Fig. 8A). Axis 2, describing 33% of the variation in data was negatively correlated with clay content and positively correlated with soil water content, and highly correlates with soil degradation intensity (eroded soils show outcropping dense and clayey B horizons). The gross $\text{CO}_2\text{-C}$ emissions decreased with decreasing soil degradation. The other PCA shows that axis 2 and axis 3 accounted for 56% of the CO_2 variation

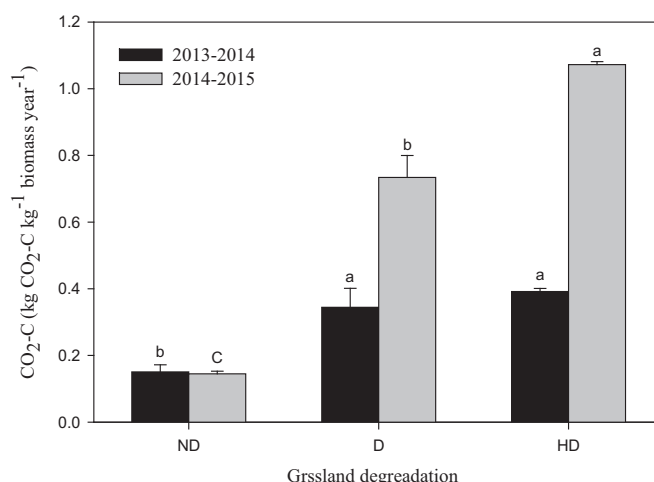


Fig. 3. Cumulative CO_2 relative to produced biomass ($\text{kg CO}_2 \text{ kg}^{-1}$ produced biomass year^{-1}) from non degraded (ND), moderately degraded (D) and highly degraded (HD) grassland. Error bars represent standard error of the mean. Different lowercase letters in each production cycle indicates significant difference between degradation levels. $N = 351$.

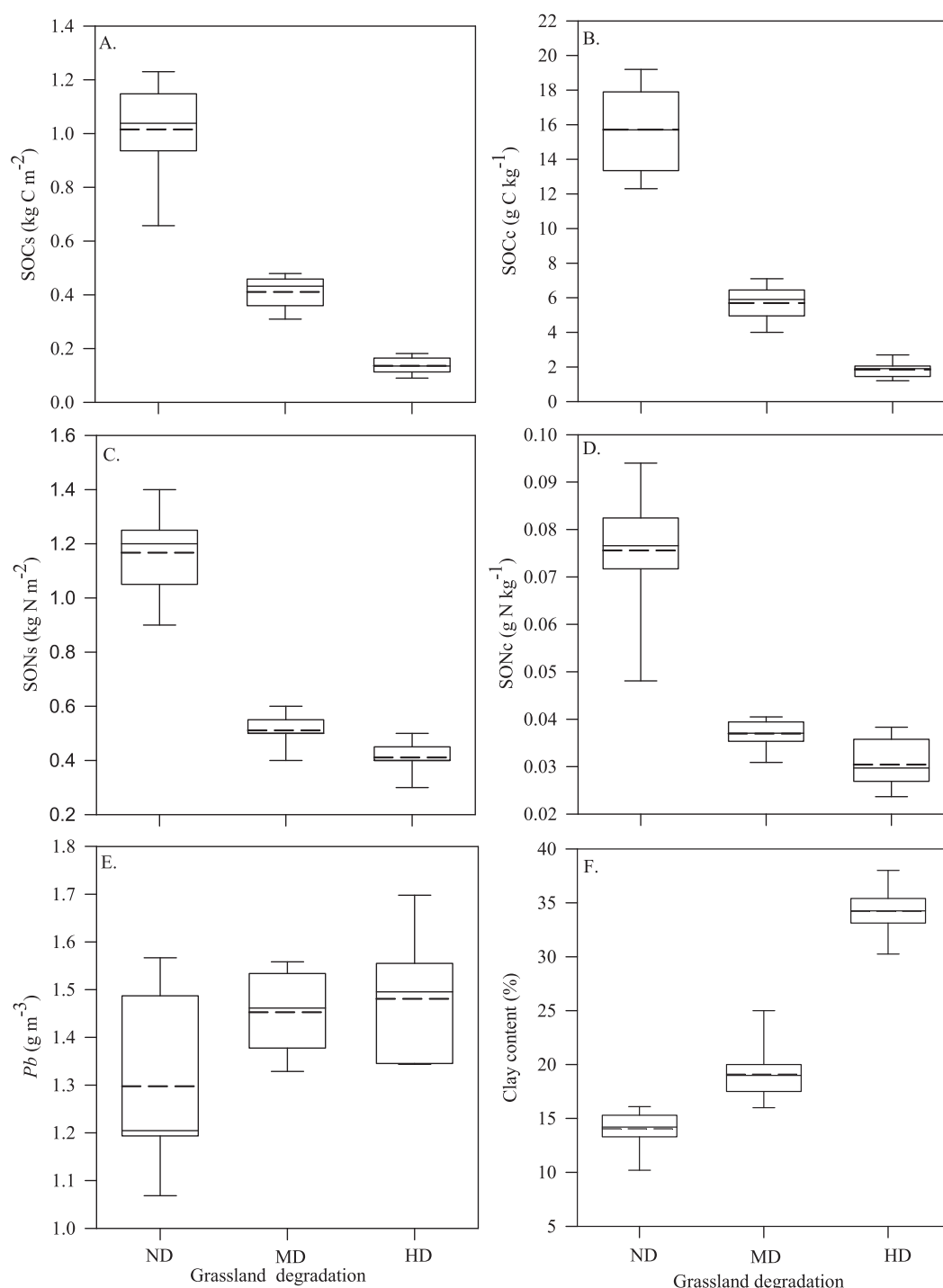


Fig. 4. Grassland degradation (ND: non-degraded; MD: moderately degraded and HD: highly degraded) impact on (A) soil organic carbon stocks (SOC_s); (B) soil organic carbon content (SOC_c); (C) soil organic nitrogen stocks (SON_s); (D) soil organic nitrogen content (SON_c); (E) soil bulk density (ρ_b) and (F) clay content in 0–0.05 m soil layer. Plan lines corresponded to 10th, 25th, median, 75th and 90th percentiles and dashed lines to the mean, N = 9.

(Fig. 8B). In this PCA, SON_c content, SOC_c and SOC_s, aboveground biomass, C:N ratio and SON stocks correlated negatively to gross CO₂ and positively to CO₂ relative to SOC_s, pointing to the increase of CO₂ emissions from soils as the intensity of grassland degradation increases.

4. Discussion

This study results point to a decrease in gross soil CO₂ emission (CO₂-C per surface area) as grass cover decreases, meaning that grass soil CO₂ emission decreased with increasing grassland degradation

(Table 1; Fig. 1C), which agreed with findings by other studies such as Wang et al. (2010), Rey et al. (2011) and Traoré et al. (2015). The non-degraded grassland emitted 11 and 62% more gross CO₂ than the moderately and highly degraded grassland, respectively. This trend can be explained by decreasing root and microbial respiration, as well as decreasing fresh organic matter input into the soil (Zhao et al., 2011; Li et al., 2015) because biomass production decreases with grassland degradation. High grass basal cover and aboveground biomass production are usually associated with high root biomass (Zhang et al., 2016), which in turn has significant impact on gross soil CO₂ emissions (Raich

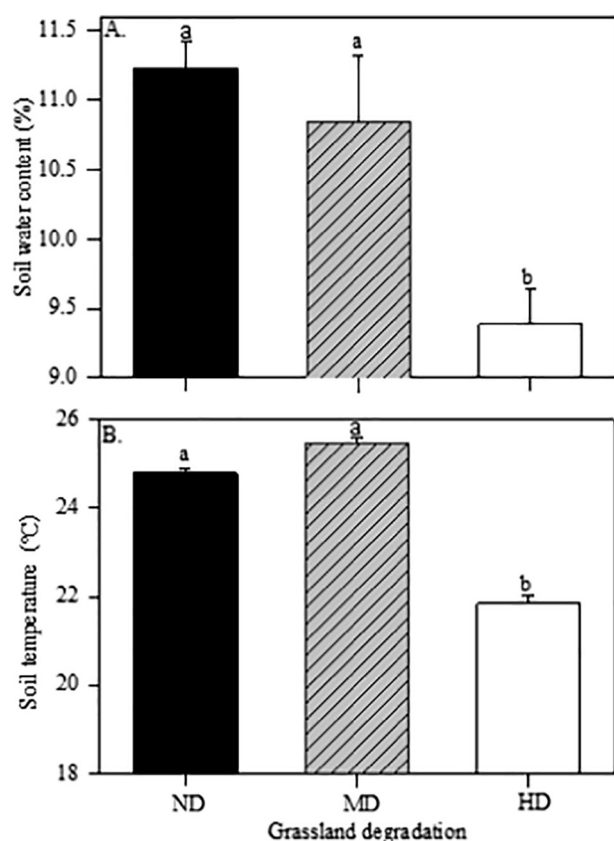


Fig. 5. Overall mean of (A) soil temperature and (B) soil water content at 0–0.05 m depth under non-degraded (ND), moderately degraded (MD) and highly degraded (HD) grasslands. Error bars represent the standard error off the mean. Different lower case letter indicates significant different ($P < 0.05$) between the degradation gradients. $N = 18$.

and Tufekciogul, 2000); Wanga et al., 2005). Studies by Raich and Tufekciogul (2000), and Wanga et al. (2005) reported that root respiration contributes between 38 and 78% of total soil CO₂ emissions.

The decrease of gross soil CO₂ emission with grassland degradation also coincided with decreasing SOC_s (Fig. 4), which pointed to significant contributions of soil C to gross soil CO₂ emissions ($r = 0.82$ and 0.83 for SOC_c and SOC_s, respectively) (Table 2). In addition, higher soil C stimulates higher microbial activity with, as reported by Whitaker et al. (2014), in a study conducted along the Andes-to-Amazon elevation gradient, increased soil respiration. The positive correlation between grassland degradation and soil clay content can be explained by the outcropping of deep clayey horizons to the soil surface thus leading a greater top-soil clay content. Such an increase in soil clay content might improve carbon protection thus depressing gross soil CO₂ emission (Traoré et al., 2015). Traoré et al. (2015) reported decreasing soil CO₂ emission with increasing soil clay content in a semi-arid climate of West Africa, which the authors attributed to the improved physical protection of soil C by clay materials. However, Li et al. (2015) reported significantly positive correlation between soil CO₂ emission and clay content in the Qinghai-Tibetan Plateau of China, which contradicts the current result.

Other factors such as soil bulk density, which Chaplot et al. (2015) showed to significantly decrease soil CO₂ emissions under a maize production system, appeared to have no significant effect on soil CO₂ emission in the current study. However, top-soil C:N ratio correlated positively with gross soil CO₂ emission, which agreed with findings by several previous studies (e.g. Whitaker et al., 2014; Spohn, 2015; Abdalla et al., 2016). Spohn (2015) explained such positive correlation in terms of three microbial mechanisms; nitrogen mining, overflow respiration, and enzyme inhibition.

Soil CO₂ emissions relative to SOC_s were 41 and 15% higher in moderately and highly degraded grassland, respectively, than non-degraded grassland (Table 1 and Fig. 2), which suggested decreasing soil C protection with increasing grassland degradation. Decreasing soil C protection with land degradation can be explained by weakening soil structure and lower aggregate stability (Mchunu and Chaplot, 2012; Chaplot and Cooper, 2015). Weaker soil aggregates offer less protection to the entrapped carbon against decomposers (Six et al., 2002), which facilitates faster decomposition of soil organic materials. Surprisingly, highly degraded grassland emitted significantly lower soil CO₂ relative to SOC_s than the moderately degraded grassland (Table 1), which coincided with significantly lower soil temperature and water content

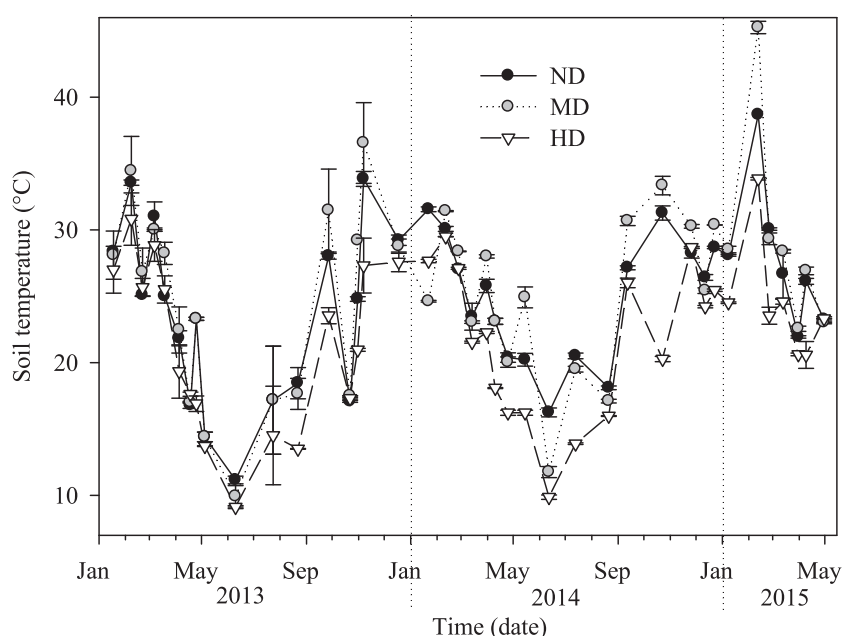


Fig. 6. Seasonal pattern of soil temperature at 0–0.05 m soil layer over the study period from non-degraded (ND), moderately degraded (MD) and highly degraded (HD) grassland. Different lower case letter indicates significant different ($P < 0.05$) between the degradation gradients. $N = 9$.

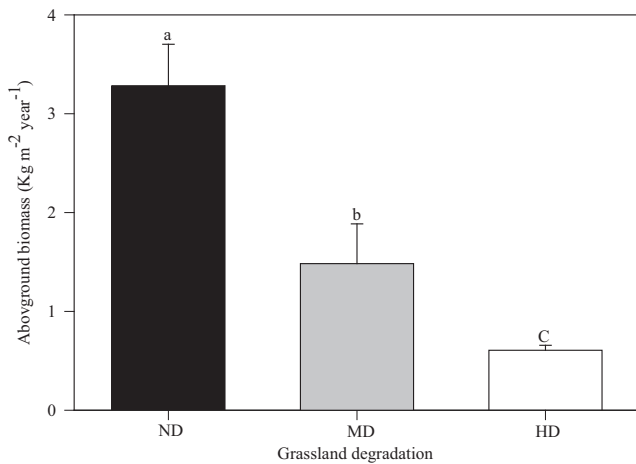


Fig. 7. Mean \pm standard error of aboveground biomass from non degraded (ND), moderately degraded (MD) and highly degraded (HD) grassland. Different lower case letter indicates significant different ($P < 0.05$) between the degradation gradients. $N = 18$.

(Fig. 5). Li et al. (2015) pointed that lower soil temperature results in lower mineralization rates of soil organic materials, hence lower soil CO₂ emissions. In addition, soil environments characterised by desiccated conditions and very low soil organic materials are likely to emit lower CO₂ amounts due to lower soil microbial activities (Fontaine et al., 2003).

The moderately and highly degraded grasslands also emitted significantly higher soil CO₂ emissions relative to amount of aboveground biomass produced per year than the non-degraded grassland (Table 1 and Fig. 3), despite significantly lower SOC_s (Fig. 4A) and biomass production (Fig. 7) than non-degraded grasslands. The foregoing result suggests for every unit of C stabilized in the soil and aboveground biomass produced, non-degraded grasslands emit less soil CO₂ in comparison to degraded grasslands. In other words, non-degraded grasslands are economical than degraded grasslands with respect to C usage. Given that grassland degradation is associated with other environmental challenges such as soil erosion and limited biomass productivity to support livestock production, proper management of

grasslands is important for water security and economic emancipation of rural communities, in addition to climate change mitigation.

The study results showing a general decrease of soil temperature and gross soil CO₂ emission with grassland degradation (indicated by reduction in grass basal cover) did not confirm the proposed hypothesis. However, soil CO₂ emission relative to SOC_s and produced biomass still showed a general increase with grassland degradation suggesting that other controlling factors, than soil temperature, had greater effects. Further studies covering diverse environmental conditions are necessary to identify and quantify the impact of factors with the most significant impact on grassland soil CO₂ emissions relative to SOC_s and biomass produced.

5. Conclusions

Three main conclusions can be drawn from this study performed on South African grasslands with the aim was to evaluate the impact of loss of grass basal cover on soil CO₂ emissions. The first one is that grassland degradation significantly decreases gross soil CO₂ emission (the emissions per surface area), with current results showing 11 and 62% lower emission in moderate (25 < grass basal cover < 50%) and highly degraded (0 < grass basal cover < 5%) than non-degraded grassland (grass basal cover: 100%), which correlated significantly with soil organic carbon and nitrogen stocks. The second conclusion is that grassland degradation increases soil CO₂ emission relative to soil carbon stocks, which imply decreasing soil organic matter protection against decomposers as grass basal cover decreases. The current study results showed at least 41% more soil CO₂ emission relative to soil carbon stocks in degraded than non-degraded grassland. The third conclusion is that grassland degradation also increase soil CO₂ emission relative to biomass produced, with the study showing 613% more CO₂ emission relative to biomass produced in degraded than non-degraded grassland. Thus, grassland degradation has a significant negative C footprint. However, these results still need validation by performing longer-term investigations at other study sites with different soil and environmental conditions. In particular, research is required to investigate further the possible underlying reasons for enhanced soil CO₂ emission relative to soil organic carbon stocks following grassland degradation. Such investigations could focus on the potential roles of (i) decreasing aggregate stability; (iii) production of easily decomposable organic

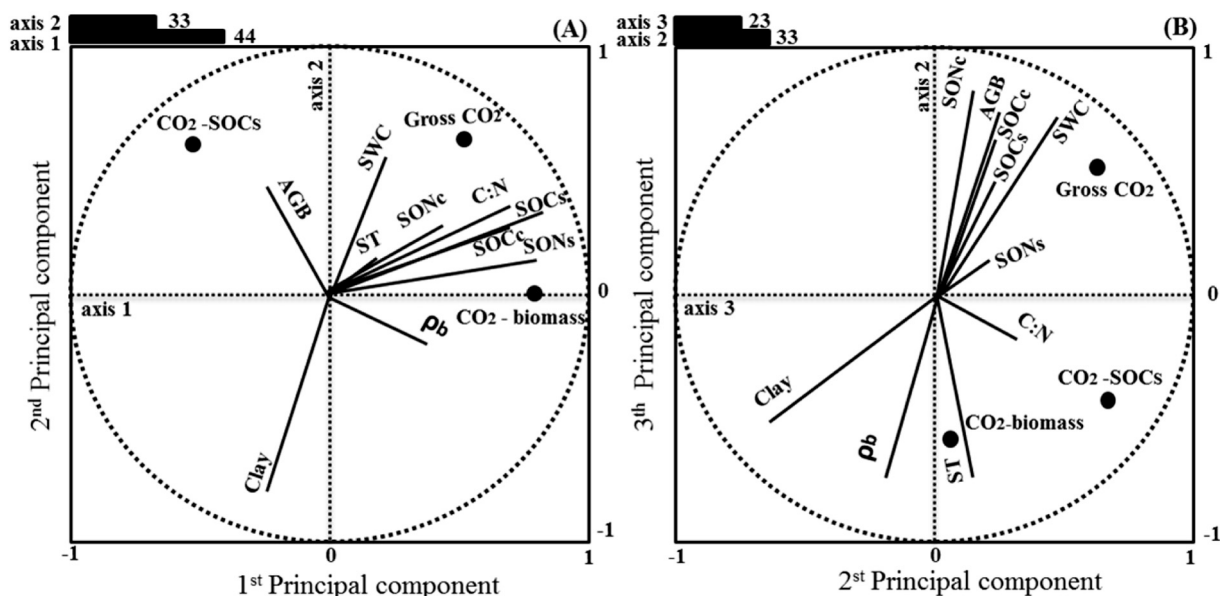


Fig. 8. Principal components analysis (PCA) scatter diagrams for gross CO₂ emissions (gross CO₂), CO₂ emissions relative to soil organic carbon stocks (CO₂-SOC_s) and CO₂ relative to produced biomass (CO₂-biomass) as supplementary variables and selected factors as active variables. (A) scatter diagram with the two first PCA axes (axis 1 and 2); (B) scatter diagram with axis 2 and 3.

products; and (iii) changes of surface albedo, soil temperature, and water content, amongst others. Further research is also needed to identify and promote suitable grassland rehabilitation techniques, which improve biomass productivity while at the same time limiting overall CO₂ emissions from grasslands soils.

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